

## Recto-tergal Fusion in the Braconinae (Hymenoptera: Braconidae): Structure and Distribution

DONALD L. J. QUICKE, ROBERT A. WHARTON AND HELGA SITTERTZ-BHATKAR

(DLJQ) Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.; (RAW) Department of Entomology, Texas A&M University, College Station, Texas 77843, USA; (HS-B) Electron Microscopy Center, Texas A&M University, College Station, Texas 77843, USA

---

*Abstract.*—A unique morphological feature is described, in which the rectum in the males of some genera of the braconid wasp subfamily Braconinae is fused with the 7th metasomal tergum. The area of the tergum overlying the area of recto-tergal fusion has a sponge-like structure in transverse section, and pores are visible using scanning electron microscopy, suggesting that this may permit volatile substances produced in the gut to escape when the wasp exposes the dorsal surface of the tergum. The distribution of this structure among the genera of Braconinae is discussed from a phylogenetic perspective.

---

### INTRODUCTION

The braconid wasp subfamily Braconinae is a diverse group containing more than 250 valid genera and 2000 described species (Shenefelt 1978; Quicke 1987; Shaw & Huddleston 1991), the majority from the Old World tropics. Members of the subfamily are almost exclusively idiobiont ectoparasitoids of concealed hosts, principally belonging to the Coleoptera and Lepidoptera, though Diptera and Hymenoptera are also attacked by some species. During surveys of the male genitalia (Quicke 1988a) and metasomal glands (Quicke 1991), we encountered an apparently unique feature of the digestive tract in members of several genera: the rectum of the male being fused dorsally to the eighth abdominal (7th metasomal) tergum. In this paper we describe the structure and ultrastructure of this anatomical feature, which we term recto-tergal fusion, and provide data on its distribution within the subfamily.

### MATERIALS AND METHODS

Morphology of the region showing the recto-tergal fusion (RTF) was studied us-

ing *Atanycolus ulmicola* (Viereck). Live males of this species were collected around dead tree trunks in Boston, Massachusetts in August of 1987, and at College Station, Texas, in September of 1987. Specimens used for light, scanning (SEM) and transmission electron microscopy (TEM) were first dissected in sterile insect saline (Ephrussi and Beadle 1939) to isolate the posterior metasomal terga and digestive tract. Terga used for SEM were separated to expose the region fused to the rectum, dried through 100% ethanol, and coated with gold-palladium, prior to scanning. Additional SEM studies were performed on pinned specimens of several other genera (*Hemibracon* Szépligeti, *Rhadinobracon* Szépligeti, *Rhytimorpha* Szépligeti).

Preparations for TEM and light microscopy were fixed for approximately 5 hours in a mixture of 2% glutaraldehyde, 2% paraformaldehyde, 2% acrolein and 1.5% dimethyl sulphoxide in 0.133 M sodium cacodylate buffer (pH 7.4). After three rinses in 0.1 M sodium cacodylate, material was post-fixed in 1% osmium tetroxide for TEM (Hayat 1989). Following fix-

ation, the material was embedded in Araldite 502-EMBED 812 Embedding Medium (Mollenhauer 1964). Semi-thin sections of 1  $\mu\text{m}$  thickness for light microscopy were stained with 0.1% toluidine blue in 1% aqueous sodium borate, and photographed with a Zeiss Axiophot using Ektachrome 160 Tungsten film. Ultrathin sections (50–70 nm) were post-stained with alcoholic uranyl acetate solution for 30 minutes followed by Reynolds' lead citrate (Reynolds 1963) for 10 minutes. Sections were examined and photographed using a Zeiss 10C transmission microscope at 60 kV on Kodak Electron Microscope Film 4489 (ESTAR Thick Base).

For a survey of the presence or absence of RTF across the subfamily, we used both live material and pinned museum specimens. Live material from field collections or from colonies maintained at Texas A&M were dissected in physiological saline. Metasomata were removed from dry specimens and soaked overnight in aqueous 10% potassium hydroxide, the sternites and tergites teased apart, and the chitinous lining of the hind gut stained with 1% aqueous Chlorazol Black. Gross dissections of all material, when performed carefully, did not disrupt the RTF, and the rectum remained tightly bound to the eighth abdominal tergum. Specimens in which RTF did not occur were unambiguously identifiable.

Suprageneric classification follows Quicke (1987). Voucher specimens of *A. ulmicola* are housed in the Texas A&M University Collection. Names of species in the genera surveyed for the presence of RTF, and their repository, are available from the senior author.

## RESULTS AND DISCUSSION

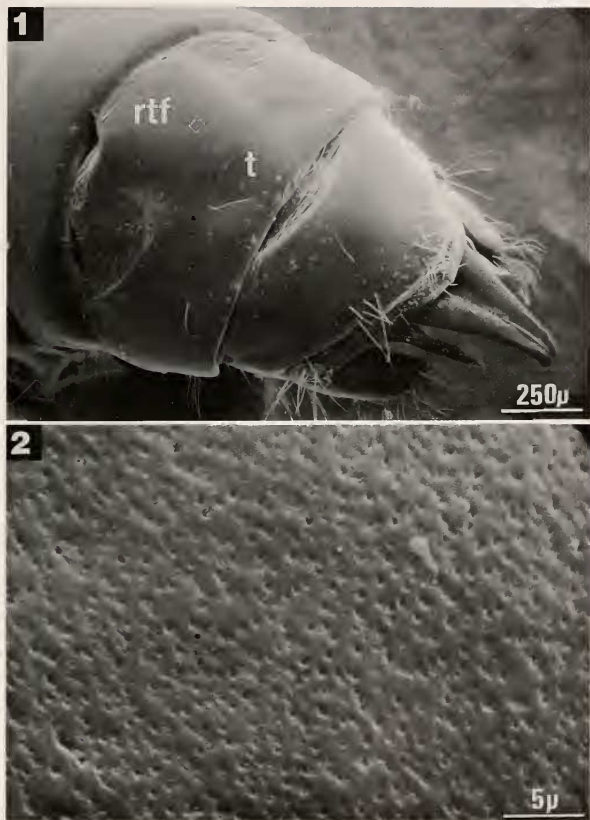
### Morphology

In living *A. ulmicola*, RTF is evident externally as a pale, circular region anteromedially on the otherwise reddish eighth abdominal tergite. Scanning electron mi-

crographs of this region in all genera examined showed the region of RTF to be sculptured differently from adjacent parts of the tergum, having numerous tiny pores (Figs 1, 2), but no other evidence of differentiation was noted. Light microscopy shows the digestive tract to be intimately associated with the tergum in the RTF region, with pores visible in the epicuticle at high magnification (Fig. 4). The cuticle over most of the region of RTF is markedly thicker in cross-section than in adjacent, lateral portions of the tergum (Figs 3 & 4). Transmission electron microscopy of the RTF region (Figs 5, 6) shows that the thickening of the cuticle is due to the development of a thick spongy layer below a thin, more or less normal fibrous layer at the dorsal surface. This spongy layer appears at higher magnification (Fig. 6) to consist largely of empty space with a three-dimensional lattice-work of chitinous rods. Whilst none of our ultrathin sections showed it, we suspect that the lumens of the dorsal pores connect directly with the spaces in this spongy layer. Towards the inner side of the tergum, the chitin becomes more coherent and the spaces are reduced, but the chitin does not reach the same density as at the outer surface (Figs 4, 5). Immediately below, and normally firmly attached to, the RTF region of the tergum is the thin chitinous membrane of the rectum; in Figure 4 the membrane has become partially detached from the tergum due to the mechanical stresses imposed by dissection and sectioning. TEM shows unambiguously that there is no living tissue between the thin cuticle of the rectum and that of the tergum within the RTF region, though elsewhere, the chitinous cuticle and the rectum wall are both lined with cells.

### Distribution

More than 20 individual males of *A. ulmicola* were dissected and no intraspecific variation was detected, all displaying RTF. We have never observed RTF in females,



Figs. 1, 2. Scanning electronmicrographs of the 7th metasomal tergum of a male *Hemibracon* sp. 1, whole tergum with area of recto-tergal fusion exposed and apparent as a weakly raised oval area; 2, detail of area indicated by white rectangle in Fig. 1. Abbreviations: rtf, recto-tergal fusion; t, 7th metasomal tergum.

Table 1. Genera of Braconinae with males that display recto-tergal fusion. Genera are arranged according to tribes and generic groups, numbers of species examined (N)

Taxon	Author	N	Taxon	Author	N
<b>Aphrastobraconini</b>			<b>Euurobraconini (part)</b>		
<i>Aphrastobracon</i>	Ashmead	2	<i>Archibracon</i>	Saussure	2
<i>Curria</i>	Ashmead	1	<i>Fraterarchibracon</i>	Quicke	1
<i>Ligulibracon</i>	Quicke	1	<i>Serraulax</i>	Quicke	1
<i>Megalommum</i>	Szépligeti	2	<i>Soronarchibracon</i>	Quicke	1
<i>Undabracon</i> (part)	Quicke	1	<b>Glyptomorphini</b>		
<i>Vipiellus</i>	Roman	2	<i>Glyptomorpha</i> s.s.	Holmgren	3
<b>Atanycolus group</b>			<i>G. (Teraturus)</i>	Kokujev	1
<i>Alienoclypeus</i>	Shenefelt	1	<i>G. (Zanporia)</i>	Sarhan & Quicke	1
<i>Atanycolus</i>	Foerster	3	<i>Rhytimorpha</i>	Szépligeti	2
<i>Calobracon</i>	Szépligeti	1	<i>Vipio</i>	Latreille	5
<i>Chaoilla</i>	Cameron	2	<b>Unplaced genera</b>		
<i>Hemibracon</i>	Szépligeti	3	<i>Campyloneurus</i>	Szépligeti	3
<i>Monilobracon</i>	Quicke	1	<i>Cordibracon</i>	Achterberg	1
<i>Nedinoschiza</i>	Cameron	2	<i>Cratobracon</i>	Szépligeti	1
<i>Neohelcon</i>	Szépligeti	1	<i>Digonogastra</i> (part)	Viereck	3
<i>Odontoscopus</i>	Kriechbaumer	2	<i>Nesaulax</i> (part)	Roman	1
<b>Bathyaulacini (part)</b>			<i>Pachybracon</i>	Cameron	1
<i>Bathyaulax</i>	Szépligeti	2	<i>Plaxopsis</i>	Szépligeti	1
<i>Euvipio</i>	Szépligeti	2	<i>Shelfordia</i>	Cameron	1
<i>Ischnobracon</i>	Baltazar	1	<i>Soter</i> (part)	Saussure	1
<i>Nundinella</i> (part)	Szépligeti	1	<i>Syltibracon</i>	Quicke	1
<i>Odesia</i>	Cameron	2	<i>Vomeribracon</i>	Quicke	1
<i>Stenobracon</i>	Szépligeti	2	<i>Zaglyptogastra</i>	Ashmead	2

although females of the great majority of braconine genera were examined. Further, RTF appears to be restricted to the Braconinae, members of virtually all other subfamilies of Braconidae having been dissected. Within the Braconinae, RTF has been found in somewhat fewer than half of the genera investigated (cf. Tables 1, 2). Within most genera it is either universally present or consistently absent, but variation was found in a few genera (*Digonogastra* Viereck, *Nesaulax* Roman, *Nundinella* Szépligeti, *Soter* Saussure, *Undabracon* Quicke). Of these, *Soter* may be polyphyletic as currently constituted, and this may also be the case with *Digonogastra* which is a very large and diverse genus. However, *Nesaulax*, *Nundinella*, and *Undabracon* are well supported monophyletic taxa (Quicke 1987; Quicke & Tobias 1990; Chishti & Quicke 1995), and therefore, it appears that RTF can be lost or perhaps

independently gained in some clades. At a higher level, the distribution of RTF appears to agree well with tribes and supra-generic groupings based on other characters (Quicke, 1987), being present, for example, in virtually all members of the *Atanycolus* Foerster group, the Bathyaulacini, Eurobraconini, and Glyptomorphini, while it is absent in all the Braconini, and the *Compsobracon* Ashmead, *Mesobracon* Szépligeti, and *Virgulibracon* Quicke groups.

## DISCUSSION

The apparent absence of RTF in all other braconid subfamilies suggests that it should be regarded as a synapomorphy within the Braconinae. Unfortunately, tribal boundaries within the Braconinae are far from settled at present, and although there are a small number of fairly clearly defined tribes, the affinities of the

Table 2. Genera of Braconinae with males not displaying recto-tergal fusion. Genera are arranged according to tribes and generic groups; numbers of species examined (N)

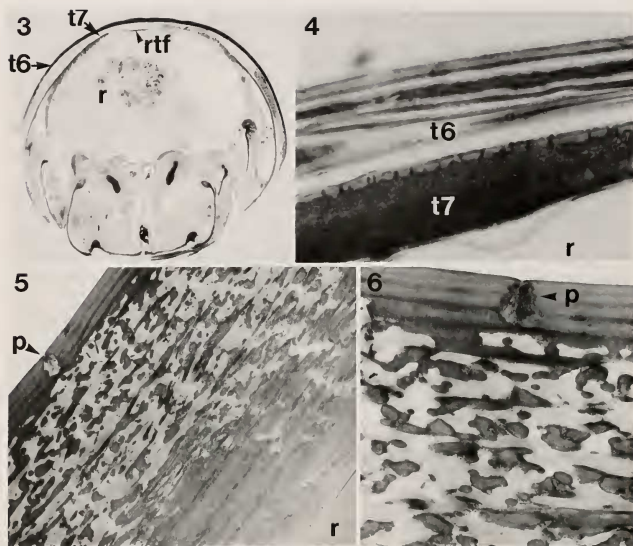
Taxon	Author	N	Taxon	Author	N
Adeshini			Coeloidini		
<i>Indadesha</i>	Quicke	1	<i>Coeloides</i>	Wesmael	1
Aphrastobraconini (part)			Eurobraconini (part)		
<i>Undabracon</i> (part)	Quicke	1	<i>Eurobracon</i> *	Ashmead	6
Bathyaulacini (part)			Iphiaulacini s.s.		
<i>Nundinella</i> (part)	Szépligeti	1	<i>Iphiaulax</i>	Foerster	6
Braconini sensu Achterberg			<i>Hybogaster</i>	Szépligeti	1
Aspidobraconina			Compsobracon group		
<i>Aspidobracon</i>	Achterberg	1	<i>Compsobracon</i>	Ashmead	2
<i>Philomacroploea</i>	Cameron	1	<i>Compsobraconoides</i>	Quicke	1
Braconina			<i>Cyclaulacidea</i>	Quicke & Delobel	1
<i>Bracon</i>	Fabricius	7	<i>Cyclaulax</i>	Cameron	1
<i>Braconella</i>	Szépligeti	1	<i>Gracilibracon</i>	Quicke	1
<i>Cratocnema</i>	Szépligeti	1	<i>Sacirema</i>	Quicke	1
<i>Habrobracon</i>	Ashmead	1	Mesobracon group		
<i>Kimavu</i>	Quicke	1	<i>Macrobracon</i>	Szépligeti	1
<i>Tropobracon</i>	Cameron	1	<i>Mesobracon</i>	Szépligeti	1
Myosoma group			<i>Mesobraconoides</i>	Sarhan & Quicke	1
<i>Myosoma</i>	Brullé	3	<i>Pseudoshirakia</i>	Achterberg	1
<i>Myosomatoides</i>	Quicke	1	Unplaced genera		
<i>Calcaribracon</i>	Quicke	2	<i>Bacuma</i>	Szépligeti	1
Physaraina			<i>Baryproctus</i>	Ashmead	1
<i>Physarainia</i>	Shenefelt	1	<i>Callibracon</i>	Brullé	2
<i>Trispinaria</i>	Quicke	1	<i>Cervellus</i>	Szépligeti	1
Pycnobracon group			<i>Cyanopterus</i>	Haliday	2
<i>Bicarinibracon</i>	Quicke & Walker	1	<i>Digonogastra</i> (part)	Viereck	2
<i>Chelonoogastra</i>	Ashmead	1	<i>Gammabracon</i>	Quicke	1
<i>Pycnobracon</i>	Cameron	1	<i>Gronaulax</i>	Szépligeti	1
<i>Pycnobraconoides</i>	Quicke	2	<i>Lasiophorus</i>	Brullé	1
Virgulibracon group			<i>Megabracon</i>	Szépligeti	1
<i>Mollibracon</i>	Quicke	2	<i>Nesaulax</i> (part)	Roman	1
<i>Virgulibracon</i>	Quicke	1	<i>Rhadinobracon</i>	Szépligeti	1
<i>Virgulibraconoides</i>	Quicke	1	<i>Soter</i> (part)	Saussure	1
			<i>Stigmatobracon</i>	Turner	1

\* In *Eurobracon* the rectum has a large number of small rectal pads rather than the four typical of all other Braconinae (Quicke 1989).

majority of genera are uncertain (Quicke 1987, 1988b; Chishti & Quicke 1995), and the relationships among tribes have not been established. Nevertheless, it is clear from our findings that RTF is not distributed randomly within the subfamily (Table 1), and it may be useful in helping define inter-generic relationships. The observed variability within some well-characterized genera such as *Nesaulax*,

*Nundinella* and *Undabracon* means that even its use in this respect must be treated cautiously, and that several species should be investigated before the absence of RTF within a taxon can be accepted with a reasonable degree of certainty.

The function of RTF can only be surmised at present. However, given its morphology, including the close proximity of the thin chitinous wall of the rectum to the



Figs 3-6. Transverse sections of 7th metasomal segment of *Atanycolus ulmicola* showing features of RTF. 3, photomicrograph of semithin section through whole tergum; 4, detail of tergal cuticle within region of recto-tergal fusion, showing pores in upper part of chitinous cuticle; 5, transmission electronmicrograph of tergal cuticle within region of recto-tergal fusion, showing pores in upper part of chitinous cuticle; 6, detail of a single pore. abbreviations, p, pore in 7th metasomal tergum; r, lumen of rectum; rtf, recto-tergal fusion; t6, 6th metasomal tergum; t7, 7th metasomal tergum. Note that in figures 3 and 4, the 6th metasomal tergum, which overlaps the 7th in normal resting position, is also sectioned.

highly modified, spongy and porous tergum in the RTF zone, together with the total loss of living rectum and epidermal cells, it seems very likely that the region has evolved to permit/facilitate passage of volatile compounds from the rectum through the tergum. If this is the case then RTF would be analogous to a gland, although no glandular tissue is present in the RTF region. Collectively, a considerable variety of true metasomal exocrine glands have also been discovered in brac-

onid wasps belonging to several subfamilies (Waseloh 1980; Tagawa 1983; Buckingham & Sharkey 1988; Williams et al. 1988; Quicke 1991; Field & Keller 1994), and as with RTF, many of these are limited to members of just one sex, often the males. Thus the distribution of RTF would be consistent in it having a pheromone-associated function possibly in relation to species recognition, courtship or aggregation. Much more work on pheromonal communication and pheromone glands in

braconids in general will be needed before the roles of the various glandular and non-glandular structures can be understood.

#### ACKNOWLEDGEMENTS

We thank the following for the loan of specimens for dissections: Kees van Achterberg (Nationaal Natuurhistorisch Museum, Leiden), Tom Huddleston (The Natural History Museum, London), Paul Marsh (formerly of the Systematic Entomology Laboratory, USDA/ARS, Washington D.C.), and Jenő Papp (Hungarian Natural History Museum, Budapest). We also thank J. W. Smith Jr. and P. Krauter for access to specimens which they had in culture. The Electron Microscopy Center of Texas A&M University is gratefully acknowledged for providing the facilities used for much of this study.

#### LITERATURE CITED

- Buckingham, G. R. & M. J. Sharkey. 1988. Abdominal exocrine glands in Braconidae (Hymenoptera). pp. 199-242. In V. K. Gupta (ed.) *Advances in Parasitic Hymenoptera Research*. E. J. Brill Publishing Co., Leiden. 546 pp.
- Chishti, M. J. K. & Quicke, D. L. J. 1996. A new genus and phylogenetic analysis of the Bathyaulacini and Glyptomorphini (Hymenoptera: Braconidae: Braconinae). *Systematic Entomology* 20: 73-84.
- Ephrussi, B. and G. W. Beadle. 1939. A technique of transplantation of *Drosophila*. *American Naturalist* 70: 218-225.
- Field, S. A. and M. A. Keller. 1994. Localization of the female sex pheromone gland in *Cotesia rubecula* Marshall (Hymenoptera: Braconidae). *Journal of Hymenoptera Research* 3: 151-156.
- Hayat, M. A. 1989. *Principles and Techniques of Electron Microscopy. Biological Applications*. 3rd Edition. CRC Press. 469 pp
- Mollenhauer, H. H. 1964. Plastic embedding mixtures for use in electron microscopy. *Stain Technology* 39: 111-114.
- Quicke, D. L. J. 1987. The Old World genera of braconine wasps (Hymenoptera: Braconidae). *Journal of Natural History* 21: 43-157.
- Quicke, D. L. J. 1988a. Inter-generic variation in the male genitalia of the Braconinae (Insecta, Hymenoptera, Braconidae). *Zoologica Scripta* 17: 399-409.
- Quicke, D. L. J. 1988b. The higher classification, zoogeography and biology of the Braconinae. pp. 117-138. In V. K. Gupta (ed.) *Advances in Parasitic Hymenoptera Research*. E. J. Brill Publishing Co., Leiden. 546 pp.
- Quicke, D. L. J. 1989. The Indo-Australian and E. Palaearctic braconine genus *Euurobracon* (Hymenoptera: Braconidae: Braconinae). *Journal of Natural History* 23: 775-802.
- Quicke, D. L. J. 1991. Tergal and inter-tergal glands of male Braconinae. *Zoologica Scripta* 19: 413-423.
- Quicke, D. L. J. and V. I. Tobias, 1990. New genera of braconid wasps of the subfamily Braconinae (Hymenoptera, Braconidae) from Australia. *Entomologicheskoe Obozrenie* 69(1): 164-180.
- Reynolds, E. S. 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *Journal of Cell Biology* 17: 208-212.
- Shaw, M. R. and T. Huddleston. 1991. Classification and biology of braconid wasps (Hymenoptera: Braconidae). *Handbooks for the Identification of British Insects* 7 (11): 1-126.
- Shenefelt, R. D. 1978. Braconidae 10. Braconinae, Gnathobraconinae, Mesostoinae, Pseudodicrogeniinae, Telengainae, Ypsistocerinae, plus Braconidae in general, major groups, unplaced genera and species. In C. van Achterberg & R. D. Shenefelt (eds) *Hymenopterorum Catalogus (nova editio)* 15. Junk, the Hague. pp. 1425-1872.
- Tagawa, J. 1983. Female sex pheromone glands in the parasitic wasps, genus *Apanteles*. *Applied Entomology and Zoology* 18: 416-427.
- Weseloh, R. M. 1980. Sex pheromone gland of the gypsy moth parasitoid, *Apanteles melanoscelus*: Revaluation and ultrastructural survey. *Annals of the Entomological Society of America* 73: 576-580.